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The Phytoplankton Zooplankton Link in the Lake Ontario Food Web

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ABSTRACT. *Monitoring in Lake Ontario in 1970 and 1982 demonstrated that the zooplankton community was dominated by microzooplankton, which suggested a longer, perhaps inefficient food chain. In this study, annual monitoring of the offshore region of Lake Ontario between 1986 and 1992 was used to determine if microzooplankton were still dominant despite recent changes in nutrient loading and species introductions. Microzooplankton accounted for 49.7% of the total summer zooplankton biomass while small edible phytoplankton accounted for 67.0% of the biomass during the summer. By direct* in situ *measurement using a Haney grazing chamber, rather than size grazing relationships, the relative impact of micro- and mesozooplankton grazers on phytoplankton production during the summer of 1995 was evaluated. Microzooplankton filtration rates (%/d) for 1995 were significantly higher than mesozooplankton filtration rates. Zooplankton consumed only 17.5% /d of the primary production with microzooplankton grazing representing 69.8% to 93.2% of this amount. Microzooplankton are clearly still dominant and their consumption of primary production in Lake Ontario is low. The major pathway of energy transfer can not be through the classical phytoplankton > large zooplankton > planktivore > piscivore food chain but rather through the phytoplankton > microzooplankton and presumably predacious zooplankton and fish. The longer food chain is a result of the introduction of a size-selective planktivore, the alewive, which has decreased the length and presumably lowered the consumption rate of the entire zooplankton community. This structural impact, a longer food chain, theoretically creates a higher factor of biomagnification of organic chemicals for top-level predators along with lower rates of energy transfer within the food web and suggests lower fish production than in a shorter food web.*

KEY WORDS: *Food web, microzooplankton, phytoplankton, grazing rates.*

INTRODUCTION

With a decrease in nutrient loading (Lucky 1994), subsequent decreases in nutrient concentration in the water column (Stevens and Neilson 1987), potential changes in phytoplankton composition (Makarewicz 1993), the influx of exotic species (Mills *et al.* 1993), and changes in the stocking of top level predators (Flint and Stevens 1989), information on the interactions within the food web has become crucial to understanding the functioning of the Lake Ontario ecosystem. The zooplankton community of Lake Ontario is under intense size-selective grazing pressure from planktivores, especially the abundant alewife (O'Gorman *et al.* 1987). As a result, small herbivores or microzooplankton (e.g., rotifers and *Bosmina*) characteristic of planktivore dominated systems have dominated the offshore waters of Lake Ontario from at least the 1960s to late 1980s (Johannsson *et al.* 1991). Based on literature values for grazing and zooplankton density in 1982, a tentative Lake Ontario food web model developed by Mazumder *et al.* (1992) hypothesized that energy is inefficiently transferred from primary producers to piscivores in Lake Ontario; that is, microzooplankton were not readily consumed by planktivores because of their small size and that microzooplankton did not efficiently graze on phytoplankton compared to larger zooplankton or mesozooplankton. Thus the classical pathway of energy and material movement in freshwater systems from algae to larger, herbivorous crustacean zooplankton to planktivores to predators either did not exist or was minimized to a brief period of time when mesozooplankton were observed. Instead, an extra step was postulated for the food web. Energy moved from algae to small rotifers and cladocerans, such as *Bosmina*, to cy-

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clopoid copepods and perhaps the omnivorous opossum shrimp *Mysis*, which are then eaten by planktivorous fish followed by piscivores.

Key to the conceptual food web model proposed was that microzooplankton were the dominant grazers in the system. Several questions are evaluated in this study. With several changes occurring in the system including nutrient reductions, introduction of exotic species, and changes in salmonid stocking policies in the past decade in Lake Ontario, have there been changes in the zooplankton community? Are microzooplankton still dominating the zooplankton composition? Second, the hypothesis empirically tested in the field is that microzooplankton are the major phytoplankton grazers in Lake Ontario. Evidence of uncoupling of the food web at the phytoplankton and zooplankton level is considered and the impact of zooplankton grazing on primary production of phytoplankton is evaluated. This study provides field data demonstrating that the Lake Ontario food web has not changed since at least 1970 and provides for the first time in over a decade, direct measurements of zooplankton grazing suggesting Mazumder's hypothesis is correct.

METHODS

Phytoplankton Culture

Cultures of *Chlorella vulgaris* (greatest axial linear dimension (GALD) of ~2 μm) and *Chlamydomonas debaryana* (GALD ~15 μm) from the University of Texas Collection of Algae (Starr and Zeikus 1993) were grown on Volvocacean medium (Starr and Zeikus 1993). All media for stock cultures were prepared fresh with distilled, deionized water and dispensed into autoclaved 250-mL screw cap, polycarbonate flasks. Cultures were maintained in an incubator at 20°C under fluorescent illumination (Sylvania "cool-white") with a 12 h light/dark cycle.

Uptake of ^{32}P by Phytoplankton

One week prior to the grazing experiment, *C. vulgaris* and *C. debaryana* were transferred from the stock culture to phosphorus free Bristol's medium and concentrated by repeated centrifugation, removal of supernate, and resuspension in approximately 20 mL phosphorus free Bristol's medium before dilution to a final volume of 150 mL. Cell density was determined with a Palmer-Maloney slide (Wetzel and Likens 1979). 200 μCi of ^{32}P was added to each 150 mL sample of cells and incubated for a minimum of three days to allow uptake of the isotope.

Field Grazing Experiment

^{32}P labelled *C. vulgaris* and *C. debaryana* cells were concentrated for use in grazing experiments by centrifugation and resuspension in Volvocacean medium and transported to the field in 10-mL septum bottles. On site, the Haney Grazing Chamber (Haney 1971) was loaded with a single species of radioactive phytoplankton cells, lowered to 4 meters, and triggered to close. The grazing chamber and contents were incubated for 7 minutes, retrieved, and a 10-mL subsample taken for scintillation counting. The remaining water was drained through two stacked sieves (mesh sizes of 200 μm and 35 μm). The sieves, which contained zooplankton, were immediately rinsed into bottles, narcotized with club soda, and preserved with buffered formalin. Zooplankton passing through a 200-μm filter but retained by a 35-μm filter were considered to be microzooplankton (Mazumder *et al.* 1992). Zooplankton retained by the 200-μm filter were designated mesozooplankton. The grazing chamber was then loaded with the other species of phytoplankton, and the process repeated for a total of six replicates of each phytoplankton species. All incubations were completed between 1000 and 1400 hours.

Primary Production

Primary production was determined with water collected from 4 m with a Van Dorn Water Bottle and placed into one transparent and one opaque 125-mL incubation bottle. Each bottle was inoculated with 5.0 μCi of $NaH^{14}CO_3$ solution using a continuous pipetter and incubated 4 m below the surface of Lake Ontario for approximately 4 h between the hours of 1000 and 1400. Upon retrieval, the samples were immediately placed in a dark box, packed on ice and placed inside a cooler for transport (30 to 45 min) to the laboratory.

In the laboratory, triplicate 5.0-mL subsamples were removed from each incubation bottle and placed in 25-mL glass scintillation vials. The subsamples were acidified to maintain a pH between 3.0 and 3.5 and bubbled in a vacuum chamber apparatus (Wessels and Birnbaum 1979) for 20 minutes to remove inorganic ^{14}C not taken up by cells

(Schindler *et al.* 1972) prior to the addition of 10.0 mL of ACS (Amersham) counting scintillant.

Activity available was determined from the dark bottle by counting unbubbled triplicate subsamples treated with 0.1 mL of phenethylamine to prevent loss of activity (Iverson *et al.* 1976; Weimer *et al.* 1975) followed by the addition of 10.0 mL of ACS (Amersham) counting scintillant. Estimates of daily volumetric production (mg C/m/d) were extrapolated from the 4-hr incubation measurements using the ratio of daily radiation to that of the field incubation period measured by an Eppley Pyranometer (Wetzel and Likens 1979).

Analysis of Radioactive Samples

Zooplankton were rinsed into scintillation vials followed by the addition of 10.0 mL of Opti-Fluor (United Technologies Packard) and thoroughly mixed. Five-mL subsamples of grazing chamber water was measured into scintillation vials followed by 10.0 mL of Opti-Fluor and also mixed thoroughly.

All radioisotopes were analyzed on a United Technologies Packard Minaxi TRI-CARB 4000 Series Liquid Scintillation Counter. The spectral index of internal standards (SIS) was measured between 5 and 1700 for all ^{32}P samples and count times were set at 15 minutes per sample to maintain percent deviations below 10%.

Grazing Experiments—Plankton Enumeration

All zooplankton in the grazing chamber experiments were identified and enumerated by the settling chamber procedure (Wetzel and Likens 1979) after allowing the ^{32}P to degrade to less than 1% of its original activity (14 weeks). Phytoplankton samples were collected at 4 m and preserved with Lugol's solution prior to counting by the settling chamber procedure.

The non-parametric Mann-Whitney U-test was used to test whether the filtration rates of micro- and mesozooplankton were different.

Sampling Sites—Field Experiments

Field experiments (grazing and primary production measurements) were conducted at two locations approximately 1 km (12 m depth) and 9 km (100 m depth) due north of Sandy Creek, near Hamlin Beach State Park, NY (Fig. 1) during two periods of time (26 June to 7 July 1995 and 9 to 14 August 1995). Two experiments were run during each period at two sites with two species of algae and six replicates per experiment (n = 96).

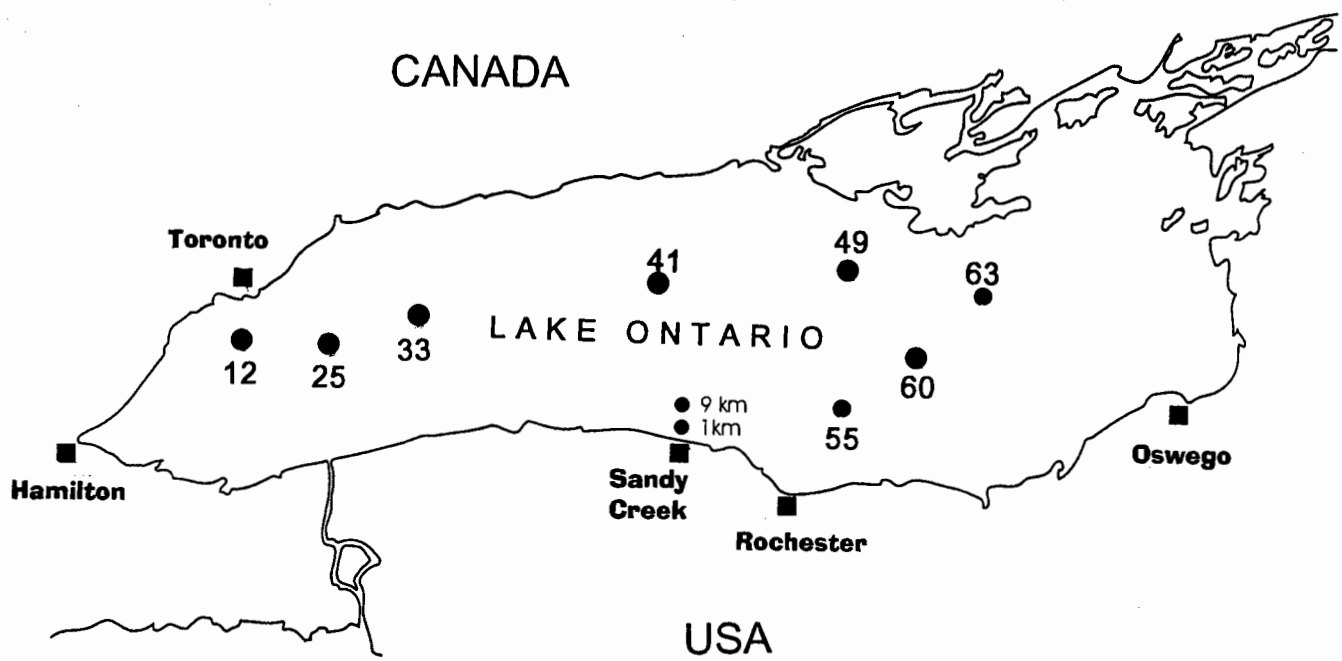

FIG. 1. Lake Ontario sampling sites showing phytoplankton and zooplankton monitoring sites (numbered) and field experimental sites labeled as the "1 km" and "9 km" stations.

Sampling Sites—Annual Monitoring

Phytoplankton

Phytoplankton were collected during a total of 23 cruises during the spring (April) and summer (August) from 1986 to 1992 at eight sampling sites (Fig. 1). The summer data are reported. An 8-L PVC Niskin bottle mounted on a General Oceanics™ Rossette sampler with a Guildline™ electrobathythermograph (EBT) was used to collect phytoplankton. Phytoplankton samples were obtained by compositing equal aliquots of samples collected at depths of 1, 5, 10, and 20 m. The species data, therefore, represent only August epilimnetic forms. Phytoplankton enumeration and biovolume calculations followed Makarewicz *et al.* (1998). Picoplankton were defined as rod or spherical shaped Cyanobacteria with a size less than 2 μm (unicells or individuals within a colony) and were not included in this report.

Zooplankton

A Wildco Model 30-E28 conical style net (62-μm mesh net; D:L ratio = 1:3) with 0.5-m opening (radius = 0.25 m) was used to collect a vertical (20 m to the surface) zooplankton sample at the same sites as phytoplankton. Only August data are presented. Filtration volume was determined with a Kahl flow meter (Model 00SWA200) mounted at 1/3 of the net diameter from one edge. Following collection, the net contents were quantitatively transferred to 500-mL sample bottles, narcotized with club soda and preserved with 5% formalin. Zooplankton enumeration and biomass calculation follow Makarewicz *et al.* (1995).

RESULTS

Phytoplankton and Primary Production

Whether expressed as abundance (all sample dates) or biovolume (except in August at the 9 km station), edible phytoplankton cells (GALD < 30 μm) dominated the phytoplankton community of Lake Ontario during the grazing studies and during the monitoring period (Tables 1 and 2). During the annual monitoring of the offshore of the lake from 1986-1992, small edible phytoplankton accounted for 67.0% of the biovolume (Table 1). Flagellates, such as *Rhodomonas* spp. *and Cryptomonas* spp., were prevalent accounting for over 12% of the abundance (Table 2). Summer midday primary production ranged from 0.9 to 10.3 mg C/m/h (mean: 4.5 mg C/m/h).

Zooplankton

Field Experiments

Zooplankton abundance and biomass were dominated by microzooplankton on all sampling dates in 1995 (Fig. 2). Rotifera comprised 38.2% while mesozooplankton comprised 11.4% of the total biomass. Similar to the monitoring sites, *Daphnia retrocurva* was the dominant mesozooplankton, while Copepoda nauplii, cyclopoid copepodites, *Bosmina longirostris*, and species of *Polyarthra* and *Keratella* were prevalent.

TABLE 1. Size and composition of phytoplankton during grazing experiments and annual monitoring (1986–1992), Lake Ontario. (GALD—greatest axial linear dimension). NS = No Sample.

	Grazing Experiment Sites				Monitoring Sites	
	June/July		August		August	
1 Km Offshore GALD	Percent Abundance	Percent Biovolume	Percent Abundance	Percent Biovolume	Percent Abundance	Percent Biovolume
30–50 μm	3.60	4.21	0.00	0.00	NS	NS
> 50 μm	2.17	34.60	0.09	35.19	NS	NS
	June/July		August		August	
9 Km Offshore GALD	Percent Abundance	Percent Biovolume	Percent Abundance	Percent Biovolume	Percent Abundance	Percent Biovolume
< 30 μm	94.28	72.93	97.53	25.97	63.20	67.00
30–50 μm	4.75	3.94	1.02	0.68	0.20	4.10
> 50 μm	0.97	23.12	1.46	73.35	36.50	28.90

TABLE 2. Summary of common August phytoplankton species occurence in Lake Ontario from 1986 to 1992 by size class. Common species were arbitrarily defined as having an abundance ≥ 0.5% of the total cells or ≥ 0.5% of the total biovolume.

Size Class: < 30 µm	Maximum	Average Abundance	% of Total Cells/mL	Mean Biovolume	% of Biovolume
	Cells/mL	Cells/mL		μm^3/mL	
Aulacoseira islandica	413	17.0	0.6	12,264	3.0
Actinocyclus normanii	201	2.3	0.1	5,987	1.5
Stephanodiscus alpinus	131	3.8	0.1	12,368	3.1
Stephanodiscus niagarae	22	1.2	0.0	17,763	4.4
Green coccoid	9,254	631.1	22.3	40,401	10.0
Chromulina sp.	213	63.4	2.2	6,587	1.6
Haptophyceae	1,439	434.2	15.3	8,167	2.0
Mallomonas sp.	8	0.3	0.0	2,989	0.7
Ochromonas sp.	573	157.1	5.5	16,478	4.1
Colorless flagellate	221	40.9	1.4	1,870	0.5
Cryptomonas erosa	245	41.8	1.5	69,330	17.2
Cryptomonas marssonii	90	17.0	0.6	11,765	2.9
Cryptomonas ovata	33	4.7	0.2	8,384	2.1
Cryptomonas phaseolus	41	5.0	0.2	2,637	0.7
Cryptomonas pyrenoidifera	65	6.9	0.2	5,162	1.3
Cryptomonas sp.	65	9.2	0.3	2,745	0.7
Rhodomonas minuta	1,325	348.1	12.3	19,443	4.8
Gymnodinium sp.	33	2.5	0.1	4,135	1.0
Peridinium sp.	57	5.2	0.2	21,484	5.3
Subtotal		1,791.7	63.2	269,959	67.0
Size Class: 30 to 50 µm					
Cosmarium depressum	16	0.6	0.0	2,971	0.7
Tabellaria flocculosa	91	6.2	0.2	13,539	3.4
Subtotal		6.8	2.4	16,510	4.1
Size Class: > 50 µm					
Fragilaria crotonensis	262	41.1	1.5	25,953	6.4
Gloeocystis sp.	720	66.1	2.3	3,512	0.9
Oocystis borgei	205	18.6	0.7	7,067	1.8
Oocystis elliptica	180	4.2	0.1	2,736	0.7
Oocystis parva	2,602	53.8	1.9	4,385	1.1
Oocystis pusilla	409	78.1	2.8	7,219	1.8
Oocystis solitaria	147	6.5	0.2	4,667	1.2
Scenedesmus bijuga	998	95.6	3.4	8,138	2.0
Scenedesmus ecornis	2,323	76.6	2.7	2,641	0.7
Sphaerocystis schroeteri	2,553	144.5	5.1	9,139	2.3
Chroococcus sp.	475	38.8	1.4	1,413	0.4
Coelosphaerium naegelianum	785	38.9	1.4	1,738	0.4
Oscillatoria limnetica	6,496	244.0	8.6	3,799	0.9
Oscillatoria sp.	924	60.4	2.1	2,231	0.6
Synechococcus sp.	1,505	66.0	2.3	3,205	0.8
Ceratium hirundinella	33	1.1	0.0	28,370	7.0
Subtotal		1,034.3	36.5	116,213	28.9

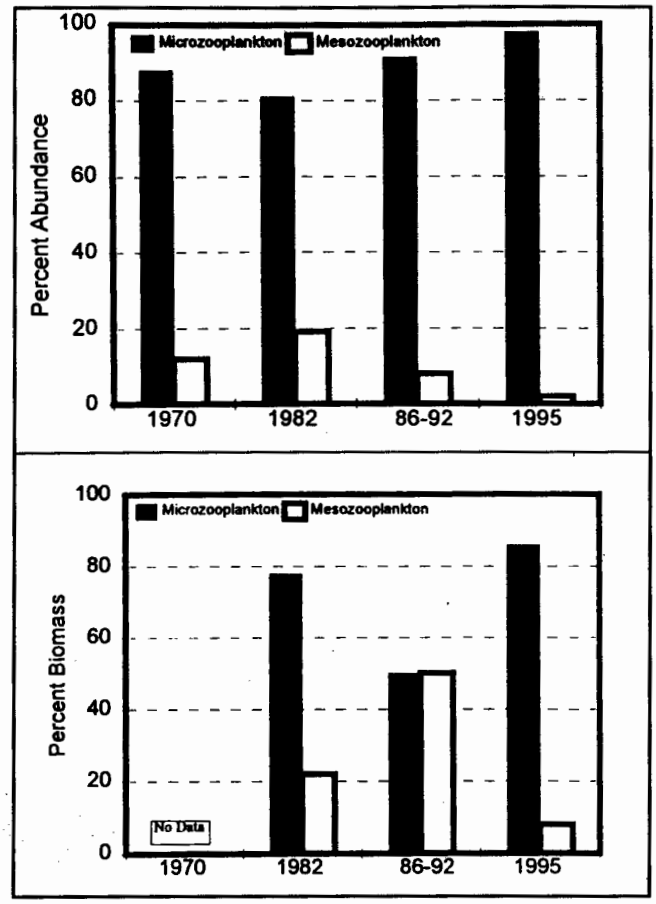

FIG. 2. Relative abundance and biomass of micro- and mesozooplankton in Lake Ontario over the past 40 years. The 1970 data [1/2 meter vertical tow, 64 μm mesh-net; Watson and Carpenter (1974)] and the 1982 data [(1/2 meter vertical tow, 64 μm mesh-net; Mazumder* et al. *(1992)] represent samples of the entire water column while the 1986-96 data (1/2 meter vertical tow, 62 μm mesh-net) are representative of the epilimnion (0 to 20 m). The Haney Chamber samples (5 L) were taken at 4 m.

Monitoring

Zooplankton collected with a vertical tow net were classified as micro- or mesozooplankton based on their classification in the field experiments derived from their retention on a 35 or 200-μm filter. Of the common species collected with a net, microzooplankton accounted for 49.7% of the total zooplankton biomass during the 7-year period of monitoring (Table 3). The most prevalent mesozooplankton were *Daphnia retrocurva* and *Daphnia galeata mendotae*. The most prevalent microzooplankton were *Bosmina longirostris*, Copepoda nauplii, Cyclopoid copepodites, *Keratella cochlearis*, and *Polyarthra vulgaris*.

Zooplankton Filtration

Zooplankton filtration rates measured from field experiments inoculated with labeled small and large algal cells from two sites on each sampling date were averaged to obtain a micro- and mesozooplankton filtration rate. Filtration rates between micro- and mesozooplankton were compared as percent of radiolabelled cells consumed per day (%/d) and as a standardized rate per unit mass of zooplankton (mL/μg/d) and per individual zooplankter (mL/ind/d)(Fig. 3). Microzooplankton grazing rates were significantly higher than mesozooplankton grazing on a %/d ($P < 0.0001$) and on a mL/μg/d basis ($P < 0.0004$) while individual grazing rates of mesozooplankton were significantly higher than microzooplankton ($P < 0.0001$). The combined micro- and mesozooplankton filtration rates, or community filtration rates, averaged 12.8%/d over the sampling period (0.96 to 68.3%/d).

DISCUSSION

Grazing rates and primary production values measured in 1995 were similar to previous reports for Lake Ontario. Epilimnetic primary production observed in 1995 (range = 0.9 to 10.4 mg $C/m^3/h$) was comparable to estimates in July of 1984/85 (1.5 to 6.7 mg $C/m^3/h$) (Nalewajko *et al.* 1989) and within the range of values (8 to 32 mg $C/m^3/h$) reported in the nearshore of Lake Ontario near Toronto (Haffner *et al.* 1988). Zooplankton community filtration rates for Lake Ontario in our 1995 study ranged from 5.2 to 18.3%/d in June/July and August, which were comparable to the range (1.7 to 26%/d) observed by Lean *et al.* (1987) for offshore stratified waters of Lake Ontario in 1982. As others (Burns and Rigler 1967, Knoechel and Holtby 1986a, Knoechel and Holtby 1986b, Peters and Downing 1984), a strong positive correlation ($r^2 = 0.88$) was observed between the average length of micro- and mesozooplankton and their filtration rates (mL/ind/d) in Lake Ontario.

A concern occasionally raised with the utilization of a low volume Haney chamber for estimating *in situ* community grazing rates is whether a representative sample of the size composition of the zooplankton community is present in the experimental chamber. Small volume samplers and even nets

TABLE 3. Summary of common zooplankton species occurrence in Lake Ontario during August,1986 to 1992. Species were arbitrarily classified as common if they accounted for ≥ 0.1% of the total abundance or ≥ 1.0% of the total biomass, with the exception of rotifers. Rotifer species were considered common if they accounted for ≥ 1.0% of the total abundance.

Monitoring Sites	Maximum Density (#/m^3)	Average Density (#/m^3)	% of Total % of Total Abundance	Mean Biomass (μg/m^3)	% of Total Biomass
Mesozooplankton					
Cyclops bicuspidatus thomasi	32,124	6,941	1.58	24,588	14.99
Cyclops vernalis	10,751	873	0.20	741	0.45
Tropocyclops prasinus mexicanus	7,715	1,102	0.25	1,286	0.78
Limnocalanus macrurus	2,077	67	0.02	1,820	1.11
Ceriodaphnia sp.	15,430	882	0.20	1,323	0.81
Daphnia galaeta mendotae	41,633	2,183	0.50	7,735	4.72
Daphnia retrocurva	131,895	13,648	3.11	39,260	23.94
		Subtotal	5.86		46.80
Microzooplankton					
Bosmina longirostris	236,790	24,893	5.67	18,046	11.00
Tropocyclops—copepodite	35,904	1,848	0.42	696	0.42
Diaptomus—copepodite	8,295	1,350	0.31	1,728	1.05
Cyclopoid—copepodite	112,288	33,348	7.59	23,064	14.06
Copepoda—nauplii	203,920	66,562	15.16	26,625	16.23
Ascomorpha ovalis	44,123	6,569	1.50	111	0.07
Conochilus unicornis	63,563	7,653	1.74	135	0.08
Kellicottia longispina	103,596	17,805	4.05	211	0.13
Keratella cochlearis	260,688	51,301	11.68	190	0.12
Keratella crassa	174,292	34,013	7.74	1,803	1.10
Keratella earlinae	134,493	14,151	3.22	377	0.23
Keratella quadrata	36,999	4,798	1.09	364	0.22
Polyarthra major	215,839	33,742	7.68	3,801	2.32
Polyarthra remata	36,207	4,523	1.03	51	0.03
Polyarthra vulgaris	290,925	86,297	19.65	3,885	2.37
Pompholyx sulcata	170,137	5,615	1.28	73	0.04
Synchaeta sp.	62,904	5,160	1.18	149	0.09
Trichocerca multicrinis	28,620	5,039	1.15	238	0.14
		Subtotal	92.14		49.7

equipped with small-mesh nets, such as used in the monitoring samples, may not adequately sample large omnivorous macrozooplankton (e.g., *Mysis*) found in Lake Ontario because of their paucity in the water column, their presence near the bottom during daylight hours and their ability to avoid a towed sampler equipped with a small-meshed net. Thus the grazing rates derived from the Haney chamber may underestimate macrozooplankton impact on community grazing rates. However, a comparison of evening biomass estimates of *Mysis* taken with a large mesh (0.57 mm-mesh net) vertical net (Shea and Makarewicz 1989) suggest that *Mysis* represents only 1 to 3% of the total zooplankton biomass when compared to the 1986-1992 biomass estimates (Table 3). Furthermore, a comparison of size composition based on numerical abundance of zooplankton from the low volume Haney chamber with the high volume vertical zooplankton tow samples taken in 1970, 1982, and 1986–92 suggest that the microzooplankton are the dominant size group in the Lake Ontario water column (Fig. 2). Even when considering biomass, percent composition of the microzooplankton represented over 85% of the zooplankton biomass in the Haney chamber samples used for estimating grazing rates-a value within the range of values (40 to 95% at three sites) observed by Mazumder *et al.* (1992) in 1982 but higher than what was observed in the vertical tows from 1986 to 1992 (average = 49.7% of

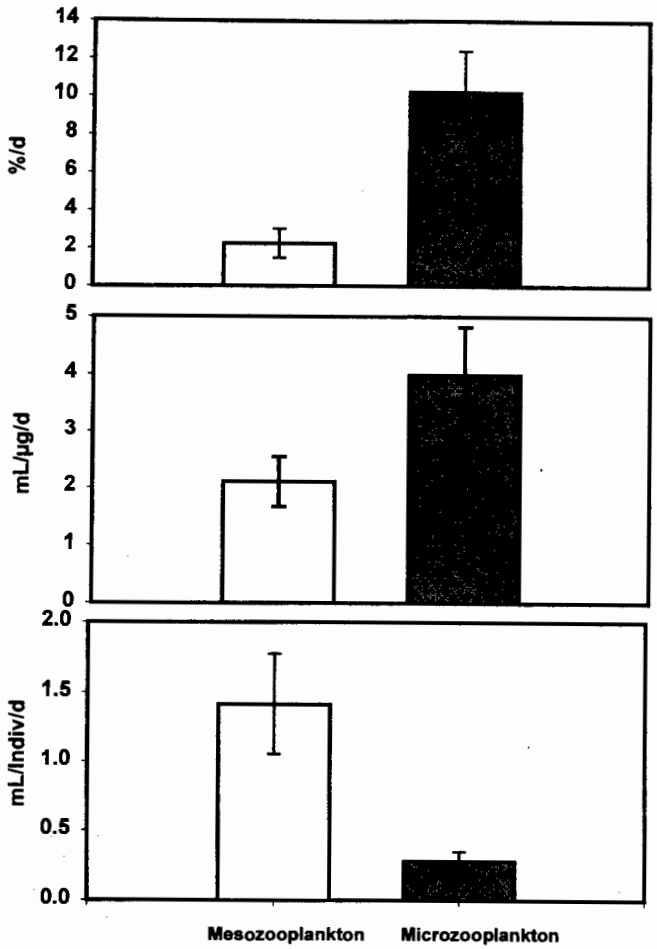

FIG. 3. Micro- and mesozooplankton filtration rates in Lake Ontario. Plotted are the average and the 95% confidence intervals. %/day is the percent of available radiolabeled cells consumed per unit time.

total biomass; Table 3). The higher value observed in the Haney chamber was not a surprising result as total counts of small volume unfiltered samples will provide higher estimates than nets equipped with a mesh greater than 30 µm, as used in the monitoring studies (Likens and Gilbert 1970, Makarewicz and Likens 1979, Mazumder *et al.* 1992).

If length of the zooplankter were the only factor that controlled filtration rate, microzooplankton would be the major grazers in the water column because of their quantitative domination. A calculation of density of a zooplankter times its filtration rate, as Mazumder *et al.* (1992) did, provides useful information on the impact on community grazing rates. However, many factors besides length affect filtration rates in microzooplankton such as shape, motility, and taste of the algae (Pace and Orcutt 1981). Since grazing rates also vary with depth, season, time of day, plankton concentration, nutrient concentration, and body of water (Cyr and Pace 1992, White and Roman 1992), application of literature values may be misleading. Thus, in a series of limited field experiments, the hypothesis that microzooplankton were the major grazers in the Lake Ontario ecosystem was tested empirically.

Although grazing rates for individual microzooplankton (mL/ind/d) in this study were significantly lower than individual mesozooplankton (Fig. 3), grazing rates for the microzooplankton community (%/d and mL/µg/d) were significantly higher than mesozooplankton grazing rates. Microzooplankton grazing represented 69.8% to 93.2% of community grazing. Similarly, Peters and Downing (1984) have observed that systems dominated by small organisms can graze more per unit biomass than one dominated by large organisms. Clearly in Lake Ontario, the major pathway of energy transfer was not through the classical phytoplankton > large zooplankton > planktivore > piscivore food chain but rather through the phytoplankton > microzooplankton and perhaps to Cyclopoid copepod and/or *Mysis* > *Mysis* > planktivore > piscivore as postulated by Mazumder *et al.* (1992).

Hartig *et al.* (1991) have suggested an uncoupling of the phytoplankton and zooplankton in the open waters of Lake Ontario; that is, the phytoplankton and zooplankton populations act independent of each other because of a mismatch in food size between zooplankton and phytoplankton. Small flagellates are preferred by microzooplankton from both a size and structure standpoint (Bogdan and Gilbert 1982) and are inefficiently grazed by larger mesozooplankton (Knoechel and Holtby 1986a, Burns and Rigler 1967). In 1995, the Lake Ontario microzooplankton community was dominated by *P. vulgaris* and *B. longirostris*, while small edible algae (< 30 µm) comprised over 90% of the phytoplankton community in the grazing studies and over 60% of the total abundance of cells in the monitoring studies (Tables 1 and 2). Flagellates predominated within the edible algae. A mismatch in food size or an uncoupling of the food chain at the phyto-zooplankton level is not suggested.

To determine the extent to which Lake Ontario's zooplankton community may be affecting the phytoplankton community, a comparison of zooplankton grazing rate (mg C consumed/m^3/d) to primary production (mg C produced/m^3/d) was made. In a

review of 44 published measurements, Cyr (1992) found that herbivores in aquatic ecosystems removed an average 51% of annual net primary production. In Lake Ontario, zooplankton were consuming only 17.5%/d (range = 3.9% to 49.6%) of the primary production. With less than 20% of the phytoplankton production being consumed, it follows that grazing pressure on small phytoplankton (< 30 μm) by the current microzooplankton community is low. This low grazing rate is probably caused by microzooplankton domination of the zooplankton community. If the same number of mesozooplankton were present, filtration and consumption rate would be greater. Low grazing loss to both micro- and mesozooplankton in Lake Ontario suggests that the zooplankton community was having a minimal effect on the phytoplankton community. Factors other than zooplankton grazing, such as cell sinking (Sagar and Richman 1991, Forsberg 1985) or nutrient limitations (Flint and Stevens 1989), may be controlling the phytoplankton abundance in the epilimnion. A second implication of a low zooplankton consumption rate of phytoplankton is that fish carrying capacity in Lake Ontario would be lower than might be expected because of the low conversion efficiency from producers to herbivores.

What are the implications of a longer food chain in Lake Ontario? An extra step in the food chain suggests that biomagnification and concentrations of chlorinated hydrocarbons in top-level predators would be higher than in systems with a shorter food chain (Cabana and Rasmussen 1994). Fish production would be lower as less energy would reach top-level predators because of the extra 90% reduction in energy flow (i.e., ecologic efficiency) imposed by an extra step in the food chain and because of the low consumption rates due to the dominant microzooplankton community. Recent discussions on adding phosphorus to Lake Ontario to stimulate salmonid fish production may be misleading in that additional phosphorus added to the system may not translate into major improvements in fish production because of the inefficient transfer of energy within this system. The end result of such a scenario may simply be accelerated eutrophication of the lake with a decrease in water quality and an increase in phytoplankton biomass with relatively little change in fish production. Similarly, Brett and Goldman (1997) concluded that under certain conditions increased primary production due to nutrient inputs may not be efficiently transferred to herbivorous zooplankton biomass. Ultimately, the cause of the longer food chain in Lake Ontario is the introduction of a size-selective feeder, the alewive (*Alosa pseudoharengus*), that removed the larger herbivorous zooplankton. Besides the well-known changes in size-structure of the zooplankton community associated with the introduction of a size-selective feeder, functional relations in the food web were also impacted with low zooplankton consumption rates of primary production, theoretically higher factors of biomagnification for top-level predators and potentially lower rates of transfer of energy leading to lower fish production.

In summary, the measurements of grazing rates in Lake Ontario reported here indicate that microzooplankton may be a major pathway of energy in the Lake Ontario food web. However, the low percentage of the primary production actually consumed suggests that the flow of energy and materials is inefficient as compared to a community dominated by mesozooplankton such as large *Daphnia*. This dominance of microzooplankton suggests that the food web in Lake Ontario may include another trophic level. Since a majority of these small herbivores are not available for consumption by planktivorous fish due to their small size, they could be consumed by larger predaceous invertebrates and theoretically increase energy flow through predators, such as Cyclopoida, *Cercopagis* sp., and/or *Mysis relicta* in Lake Onatrio.

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